

## SEX-LIMITED CHARACTERS IN HETEROSPOROUS SPOROPHYTES.\*

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It appears that sex-limited characters and sexual dimorphism have in the past been considered mostly from the animal side of the subject. For this reason it was thought advisable to give a brief account of some of the more common species which show dimorphism in the sporophyte. The gametophytes of homosporous plants also often show decided sexual dimorphism and the gametophytes of the heterosporous plants exhibit the most extreme dimorphism of any organisms, whether plant or animal.

In order to get a correct understanding of sex-limitation it is best to study sex-limited characters in monocious plants first; for in this case the factors involved can be had in the homozygous condition and the sexual state arises directly from a neutral condition in the vegetative tissues. There are also no allosomes to complicate conditions. In monocious plants the two types of flowers may be commingled in the same inflorescence as in *Aesculus glabra* or in different parts of the same inflorescence, or the inflorescences may themselves be monosporangiate and variously distributed or related to each other on the plant. Two characteristic types are the following: 1st. The staminate flowers are developed first, the inflorescence axis passing from the neutral to the male condition and later this male condition is reversed, passing thru a neutral condition over to the female condition when carpellate flowers are developed. This is the androgynous condition, as in *Carex trisperma*, *Ricinus communis*, and *Zizania aquatica*, and the progression of sexual states corresponds to the normal progression in the flower axis itself. 2nd. The carpellate flowers are developed first and the inflorescence axis changes later from the female state thru a neutral condition, to the male state when staminate flowers are produced above. This is the gynandrous condition and is just the opposite of what normally takes place in the flower axis itself of angiosperms. Examples are *Carex capita*, *Sagittaria latifolia*, *Peltandra virginica*, and *Typha latifolia*. Unfortunately these terms, or at least the first one, have been used in exactly the opposite sense in descriptive botany to designate position on the inflorescence axis.

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\* Papers from the Department of Botany, The Ohio State University, No. 170.

But it would be very confusing to say that an inflorescence or a plant was androgynous in the genetic sense when the carpellate flowers because of the female condition come first. And it is becoming more evident continually that the dead biology of the past must give way to a "living" or dynamic biology. The terms proterandrous and proterogynous are not available since they refer rather to ripening of the pollen and stigma than to the time of the development of the sporophylls on the axis.

It is evident from the sexual conditions in monocious and hermaphroditic plants that sex-limitation is not a matter of dominance and recessiveness but rather of activity and latency thru the influence of the given sexual state. With the change in sexual state in some part of the body the suppressed factors become active whenever the proper differentiation stage is attained.

Sex-limited characters in the lowest types of heterosporous sporophytes appear only in the sporangia or their stalks. In the second stage of evolution, dimorphisms appear in the sporophylls themselves and as a general rule the diversity increases with the higher types. In the third stage sexual dimorphisms appear between the staminate and carpellate flowers outside of the sporophylls themselves, and the same kinds of differences are to be observed between the flowers whether the plants are monocious or diecious. The fourth stage of evolution of dimorphism shows differences in entire inflorescences; and in the fifth step the sex-limited characters show also in the leaves and stems some distance beyond the inflorescences. In the sixth and extreme case, present typically only in diecious plants all parts of the body may show dimorphic characters in relation to sex.

Sex-limited characters, when they appear on unisexual individuals, have in the past played a prominent part in fantastic speculations on evolution by sexual selection. But when it is realized that the same dimorphisms appear in the sexually differentiated parts of hermaphrodites and monocious species and that the most extreme dimorphisms are to be found in plants which have neither eyes nor the nervous equipment with which to make a choice the whole subject of sexual selection can be easily relegated to the domain of fairyland.

Below is given a small list of the various types of sex-limited characters in heterosporous sporophytes to show the general nature of such characters in the higher plants. For sex-limited characters due to allosomes and characters which show a pecul-

iar migration or transmission because their factors are allosome-linked altho not necessarily sex-limited, one must at present go to the animals.

PLANTS WITH BISPORANGIATE SPOROPHYLLS OR WITH  
BISPORANGIATE FLOWERS.

1. *Marsilea quadrifolia*—Microsporangia with long, slender stalks; megasporangia with short, robust stalks.
2. *Selaginella kraussiana*—Microsporophyll with a smaller, acuminate blade; megasporophyll with a larger, acute blade.
3. *Aquilegia canadensis*—Carpel covered with hairs, stamen glabrous.

Small differences in character expressions of this nature are almost universal in the sporophylls of seed plants.

MONECIOUS PLANTS.

1. *Taxodium distichum*—Dimorphic inflorescences; staminate cones numerous in a slender catkin-like panicle, carpellate cones few in a small terminal cluster.
2. *Larix laricina*—Staminate flowers pale yellow, carpellate flowers rose-red; stamens and carpels structurally different.
3. *Pinus sabiniana*—Staminate flowers yellow, carpellate flowers dark purple; stamens without a special outgrowth, carpels with a special ovuliferous scale.
4. *Pinus radiata*—Staminate flowers yellow, carpellate flowers dark purple; stamens without a special outgrowth, carpels with a special ovuliferous scale.
5. *Limnobium spongia*—Staminate flowers long-peduncled; carpellate flowers sessile or with a short peduncle.
6. *Cocos nucifera*—Staminate flowers with apocarpous vestigial carpels, small sepals, and narrow petals; carpellate flowers syncarpous with very large broad sepals and broad petals.
7. *Zizania aquatica*—Lemma of staminate flower without an awn; lemma of carpellate flower with a long awn.
8. *Tripsacum dactyloides*—Carpellate part of inflorescence with modified rachis with the spikelets in deep pockets; staminate spikelets on an ordinary rachis.
9. *Euchlaena mexicana*—Decided differences between the staminate and carpellate inflorescences and their bracts; carpellate rachis extremely modified into pockets.
10. *Zea mays*—Decided sexual dimorphism between the two inflorescences and the internodes and their leaves below.
11. *Liquidambar styraciflua*—Carpellate flowers in a simple spherical head; staminate flowers in racemose clusters.
12. *Sarcobatus vermiculatus*—Staminate flowers without a calyx in scaly spikes; carpellate flowers with a compressed calyx, sessile and solitary.
13. *Eurotia lanata*—Staminate flower with a four-parted calyx; carpellate flower with two united bracts covered with long hairs.
14. *Quercus* sp. Staminate flowers without involucre, in long flexible catkins; carpellate flowers solitary or clustered, with a prominent expanded cup and involucre.

15. *Alnus* sp.—Staminate and carpellate catkins and their bracts decidedly different.
16. *Ostra virginica*—Bracts of the staminate and carpellate inflorescences decidedly dimorphic.
17. *Carpinus caroliniana*—Bracts of the staminate and carpellate inflorescences different.
18. *Juglans nigra*—Carpellate flowers solitary or several in a cluster at the end of a short peduncle; staminate flowers in long flexible catkins.
19. *Hicoria* sp.—Inflorescences with dimorphisms similar to *Juglans*.
20. *Croton capitatus*—Staminate flowers racemose with a 5-parted calyx and 5 petals; carpellate flowers sessile, with 7-12 sepals and no petals.
21. *Littorella uniflora*—Staminate flowers on slender scapes; carpellate flowers sessile.
22. *Cyclanthera dissecta*—Staminate flowers racemose on long peduncles; carpellate flowers solitary on very short peduncles.
23. *Sicyos angulatus*—Staminate flowers corymbose or racemose on a long peduncle; carpellate flowers capitate on a shorter peduncle.
24. *Ambrosia* sp.—Carpellate and staminate heads decidedly dimorphic.

EXAMPLES TO SHOW THAT SEX-LIMITED CHARACTERS ARE SIMILAR  
IN MONECIOUS AND DIECIOUS SPECIES.

1. *Naias flexilis*, monecious—Carpellate flower without a spathe, staminate flower with a double spathe or sheath.
2. *Naias marina*, diecious—Flowers of the same nature as in the monecious species.
3. *Carex lupulina* and most other species, monecious—Carpellate flowers with a sack-like perigynium; staminate flowers without a perigynium.
4. *Carex dioica*, diecious—Carpellate and staminate flowers of the same nature as in the monecious species.

DIECIOUS PLANTS.

1. *Cycas revoluta*—Staminate and carpellate plants with very extreme sex-limited characters. Carpellate plant flowerless, the carpels in a rosette, staminate plant with determinate cones. Carpels with a compound leaf blade, stamens simple.
2. *Taxus canadensis*—Carpellate flower with one reduced carpel; staminate flower with 5-8 stamens.
3. *Hydrocharis morsus-ranae*—Flowers decidedly dimorphic, the staminate and carpellate flowers on two different evolutionary levels. Staminate flower with 3 vestigial, apocarpous carpels, 9 stamens and 3 staminodes, hypogynous; carpellate flower with 6 syncarpous carpels and only 6 vestigial epigynous stamens.
4. *Vallisneria spiralis*—Carpellate flower solitary and large on a very long, spirally coiled peduncle by which the flower reaches the surface; staminate flowers minute, many on a very short peduncle, the individual flowers separated by an abscission layer and floating free on the surface.
5. *Phoenix dactylifera*—Decided dimorphism between the perianths of the staminate and carpellate flowers.

6. *Distichlis spicata*—Rachilla continuous in the staminate spikelet and the spikelets more numerous than in the carpellate inflorescence; rachilla of the carpellate spikelets articulated and the spikelets fewer in the inflorescence.
7. *Bulbilis dactyloides*—Decided dimorphism between the staminate and carpellate inflorescences and spikelets.
8. *Spinifex hirsuta*—With decided sexual dimorphism of the inflorescences.
9. *Similax herbacea*—Perianth segments of the staminate flowers larger than those of the carpellate flowers.
10. *Arisaema triphyllum*—Peduncle of the carpellate inflorescence much more persistent than that of the staminate inflorescence.
11. *Dioscorea villosa*—Carpellate inflorescence a simple catkin-like spike with few flowers; staminate inflorescence a branched panicle, the branches slender and spike-like with numerous flowers.
12. *Thalictrum dioicum*—Sepal of the carpellate flower about twice as long and wide as of the staminate flower, oval or obovate, while the sepal of the staminate flower is narrowly ovate and with a somewhat narrowed tip.
13. *Mercurialis annua*—Staminate flowers in elongated axillary spikes or racemes; carpellate flowers in the axils of the leaves.
14. *Carica papaya*—Inflorescence and flowers decidedly dimorphic; staminate flowers sympetalous in large, much branched inflorescences; carpellate flowers choripetalous in small slightly branched inflorescences or solitary.
15. *Papyrius papyrifera*—Staminate flowers in cylindric ament-like spikes; carpellate flowers capitate.
16. *Cannabis sativa*—Both the vegetative parts and the flowers with decided sexual dimorphism. In winter-grown hemp second internode of staminate plants about twice as long as that of carpellate plants.
17. *Humulus japonicus*—Both the inflorescence and the vegetative parts of the flowers show decided sexual dimorphism.
18. *Baccharis halimifolia*—Heads of the staminate and carpellate plants dimorphic.
19. *Anaphalis margaritacea*—Staminate and carpellate corollas dimorphic.
20. *Antennaria plantaginifolia*—Involucral bracts, pappus bristles, and corollas of the staminate and carpellate heads strongly dimorphic.

#### VESTIGIAL SPOROPLYLLS.

Below are given brief lists of some of the species studied by the writer to show the four possible types of distribution of vestiges of the opposite sporophylls in monosporangiate flowers. Cases in which vestiges are present in one flower and not in the other are to be regarded as sexual dimorphisms or sex-limited characters the same as dimorphisms in the vegetative parts; for the experiments on hemp and other plants show that the potentialities for both sporophylls are present

even when there is no vestige whatever expressed under normal conditions.

1. Monecious and diecious plants with sporophyll vestiges in both staminate and carpellate flowers—*Sagittaria latifolia*, monecious; *Phoenix dactylifera*, diecious; *Cocos nucifera*, monecious; *Zizania aquatica*, monecious; *Tripsacum dactyloides*, monecious; *Asparagus officinalis*, diecious; *Hydrocharis morsus-ranae*, diecious; *Chamaelirium luteum*, diecious; *Dioscorea villosa*, diecious; *Musa sapientum*, monecious; *Gymnocladus dioica*, diecious; *Lychnis alba*, diecious; *Acer platanoides*, diecious; *Rhus glabra*, diecious; *Acer saccharinum*, diecious; *Schmalzia crenata*, diecious; *Coix lacryma*, monecious; *Sassafras sassafras*, diecious; *Ailanthus glandulosa*, diecious; *Ptelia trifoliata*, diecious; *Rumex altissimus*, monecious; *Aruncus aruncus*, diecious; *Platanus occidentalis*, monecious; *Aesculus glabra*, monecious; *Cucumis sativus*, monecious; *Diospyros virginiana*, diecious; *Silphium integrifolium*, monecious.

2. Monecious and diecious plants with stamen vestiges in the carpellate flowers but without a vestige of the gynecium in the staminate flowers—*Vallisneria spiralis*, diecious; *Smilax hispida*, diecious; *Peltandra virginica*, monecious; *Zantedeschia aethiopica*, monecious; *Menispermum canadense*, diecious; *Napea dioica*, diecious.

3. Monecious and diecious plants with carpel vestiges in the staminate flowers but without stamen vestiges in the carpellate flowers—*Tumboa bainesii*, diecious; *Carica papaya*, diecious; *Ambrosia trifida*, monecious; *Rumex acetocella*, diecious; *Amaranthus retroflexus*, monecious; *Morus alba*, diecious.

4. Monecious and diecious plants with no vestigial sporophylls normally either in the staminate or carpellate flowers. In general none of the primitive types of flowers like *Pinus*, *Zamia*, or *Juniperus* show any indication of the opposite type of sporophylls and frequently the extreme types of monocotyls and dicotyls also show no such vestiges. Occasionally low types of diecious angiosperms also show no vestiges like the diecious or partially diecious *Thalictrums* altho they have plainly been derived from bisporangiate ancestors like the *Thalictrums* with bisporangiate flowers—*Alocasia odorata*, monecious; *Arisaema triphyllum*, diecious; *Typha latifolia*, monecious; *Carex* sp., monecious and diecious; *Thalictrum dioicum*, diecious; *Cannabis sativa*, diecious; *Humulus japonicus*, diecious; *Acer negundo*, diecious; *Populus deltoides*, diecious; *Begonia* sp., monecious; *Sicyos angulatus*, monecious.